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False holes as camouflage

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Abstract

Long noted by naturalists, leaf mimicry provides some of the most impressive examples of camouflage through masquerade. Many species of leaf-mimicking Lepidoptera also sport wing markings that closely resemble irregularly shaped holes caused by decay or insect damage. Despite proposals that such markings can either enhance resemblance to damaged leaves or act to disrupt surface appearance through false depth cues, no attempt has been made to establish exactly how these markings function, or even whether they confer a survival benefit to prey. Here, in two field experiments using artificial butterfly-like targets, we show that false hole markings provide significant survival benefits against avian predation. Furthermore, in a computer-based visual search experiment, we demonstrate that detection of such targets by humans is impeded in a similar fashion. Equally contrasting light marks do not have the same effect; indeed, they lead to increased detection. We conclude that the mechanism is disruption of the otherwise homogeneous wing surface ('surface disruptive camouflage') and that, by resembling the holes sometimes found in real leaves, the disruptive benefits are not offset by conspicuousness costs.

Keywords: protective coloration, camouflage, predation, surface disruption, leaf mimicry, depth perception.

1. Introduction

Leaf mimicry is a taxonomically widespread form of the camouflage strategy known as masquerade: resemblance to an irrelevant background object [1-4]. This impressive example of protective coloration has been discussed by naturalists and evolutionary biologists for more than a century [5,6]; not only do many animals bear a remarkable resemblance to the shape of a leaf but, in many cases, they also exhibit marks that look like the blemishes of decay or products of attack by herbivores (figure 1). For example, Alfred Russel Wallace describes this phenomenon first hand in his seminal work on mimicry and other protective resemblances noting: "… we find representations of leaves in every stage of decay, variously blotched and mildewed and pierced with holes …" ([7], p. 7). Striking examples of such markings can be seen in several species of Anura and Lepidoptera, which closely resemble irregular holes in the wing or body surface (figure 1). Although some are simply dark, contrasting, colour patches, other markings are so convincing in apparent 3D relief (at least in a photograph) that the holes look real. However, rather like another striking form of defensive coloration, 'eye spots' [8], the term 'false hole' suggests a function that it is dangerous to assume without evidence [9]. Until now, there have been no investigations of whether false holes are even adaptive and, if so, by which mechanism(s) would it be advantageous to bear patterns that resemble a hole.

Unless damaged leaves are the norm, it is not immediately obvious why mimicking a leaf with holes would be a better disguise than mimicking an intact leaf. Indeed, there is some evidence that insectivorous birds can use leaf damage as a cue to the presence of caterpillar prey [10,11]: mimicking such a leaf would attract attention rather than avoid it. Both Thayer [12] and Cott [13], pioneers of camouflage theory, instead

proposed that these markings are disruptive camouflage, either breaking up the wing surface into apparent multiple planes using false depth cues, disguising shape through the creation of false internal edges with higher contrast markings than the true wing boundary, or simply distracting attention from the wing boundary. Today these putative effects are recognised as different mechanisms [3,14] and, in different contexts, there is evidence that each can be effective [1].

Here, we attempt to identify any survival advantage conferred by false hole markings, and the possible mechanism(s) by which this benefit could be achieved. We carried out three experiments using artificial butterfly-like targets: two in the field under bird predation and a third, computer-based visual search task with humans as surrogate predators. In the first field experiment, we investigated whether real holes in the wings of leaf-like prey provide a survival advantage (without such an advantage, the benefits of false holes must lie elsewhere), and whether this effect is background-dependent. In the second field experiment, we assessed the degree to which false holes affect survival relative to targets with real holes, and no holes, in the wings: real holes always look like the surface underneath, whereas false holes only represent one generic background. We also explored whether this benefit could be achieved by any high-contrast surface marking: is mimicking a hole actually important, or is just breaking up the surface with a contrasting pattern sufficient? In the third (computer-based) experiment, we used humans to assess directly the effect of false holes on target detectability, furthering our understanding of the similarities and differences in organisation and performance of avian and human visual search.

2. Materials and Methods

(a) Field experiments with avian predation

(i) Stimuli

Prey targets were coloured paper 'wings' attached to an edible mealworm 'body'. A stencil was used to create background-matching artificial butterfly wings that were the average colour of bramble, based on calibrated digital photographs of a sample of 50 *Rubus fruticosus* leaves (following Stevens *et al.* [15]), in the colour space of a model passerine bird, the blue tit *Cyanistes caerulescens* (following Stevens *et al.* [16]). The targets were not intended to mimic any real species of butterfly (for which avian predators might have pre-existing preferences or aversions) and bramble was chosen as a substrate simply because it was common across the study site, and an easily matched homogeneous green. Target wings were printed double-sided on to A4 waterproof paper (Rite-in-the-Rain, J.L. Darling LLC, Tacoma, WA, US) using a calibrated Canon imageRUNNER ADVANCE C5535i printer (Canon Inc., Tokyo, Japan). Printing double-sided ensured that targets remained cryptic even if the wings separated from each other (see below). Wings were scored and folded down the mid-line, and glued together (Pritt original, Henkel Ltd, Germany) to replicate the appearance of a butterfly in its natural resting position. To create holes (figure 2), a nominally flower-shaped hole-punch (Woodware craft collection; Woodware, Skipton, UK) was used. This shape was chosen as a low-salience convenient shape; a circle or other simple geometric shape might have attracted attention, being rare in natural backgrounds [17].

A 30 mm x 0.5 mm dressmaking pin (PRYM, Stolberg, Germany) was inserted approximately a third of the way down the wings (figure 2). A dead mealworm

(*Tenebrio molitor* larva frozen at -80°C) was threaded onto to the pin, which was then attached to the background substrate. New targets were used for every block.

The first field experiment was designed to assess whether real holes in wings affected predation rates using two treatments, 'Intact wings' and 'Real holes'. The second field experiment introduced wing markings. This experiment used four treatments: 'Intact wings', 'Real holes', 'False holes', 'Pale controls'. To create the False hole treatment, a dark shade of grey matching the mean luminance of the background seen through calibrated photographs of the Real hole targets *in situ* was used. The Pale control was a shade of grey of equal luminance contrast to that of the False holes, with respect to the 'bramble green' base colour of the wings. This treatment served to assess whether contrast per se with the wings was responsible for a false (or real) hole's effect on predation risk, or whether that patch has to be darker than the rest of the wing surface. In Cott's [13] original formulation of his theory of 'maximum disruptive contrast', it was the contrast with background-matching colours on the animal that aided concealment, regardless of whether these colours were common in the background or not [18]. The contrasts were based on the double-cone response of a Blue Tit *Cyanistes caeruleus* [19], calculated as in Stevens *et al*. [16].

(ii) Protocol

The first field experiment was conducted on 15th-26th January 2018 and the second on 5th - 31st March 2018, both in Brandon Hill Nature Reserve, Bristol, UK (51.4541° N, 2.6065° W), a hilly and grassy 1.81-hectare urban parkland inhabited by a variety of avian predators such as Blue Tits (*Cyanistes caeruleus*), Great Tits (*Parus major*), Eurasian Wrens (*Troglodytes troglodytes*), Common Chaffinches (*Fringilla coelebs*), Common Blackbirds (*Turdus merula*) and European Robins (*Erithacus rubecula*).

The first experiment had a 2 × 2 factorial design: treatment (Intact wings, Real holes) and substrate (Bramble – pinned to the petiole of bramble leaves; and Twig – pinned to an exposed, leafless twig of young hazel (*Coryllus alevana*), ash (*Fraxinus excelsior*), elder (*Sambucus nigra*), or birch (*Betula* sp.). We expected survival to be lower on exposed twigs, as the targets were not surrounded by similarly coloured leaves. The goal was to determine whether any effect of a hole was background dependent. There were 15 targets of each treatment*substrate combination per block, with three blocks each at different locations within the study site. The second experiment had 30 targets per treatment per block with 10 blocks in different locations within the study site. The substrate was bramble.

In both experiments, plants to which individual targets were pinned were selected haphazardly, as was the position and orientation of the targets; but target selection for any one plant was random (pulled from a plastic sealable bag in which all targets for a block had been shuffled). In each block, targets were put out between 9am and 10am and checks for predation were completed after 3, 6, 24, 27, 30, 48, 51 and 54 h. A target was said to have been predated when the mealworm was absent; data were treated as censored if the target could not be relocated, the target was found on the ground with either the mealworm or wings missing, the mealworm was subject to invertebrate predation (mainly slugs, visible on the target or leaving the paper chewed), or if the target survived to the end of the three-day study period. Targets that were predated were removed and, at the end of a block, all remaining targets were collected.

(iii) Statistical analysis

To take account of censoring, in both avian experiments survival analysis of 'time to predation' was by mixed effects Cox regression using the '*coxme*' package [20] in R 3.5.3 (R Core Team 2019), with block as a random effect and the fixed factors treatment and substrate for the first field experiment, and treatment for the second field experiment. The proportional hazards assumption of the method was checked by visual inspection of partial residual plots against the ranked survival time [20]. Where interactions were not significant, main effects were estimated by refitting models without the interaction. The primary hypotheses of *a priori* interest were pair-wise comparisons with the Real holes treatment, with p-values unadjusted because the number of tests did not exceed the degrees of freedom [21]. The package *'multcomp'* [22] was used for subsequent pair-wise *post hoc* comparisons of secondary interest, using the Bonferroni method to control for multiple testing. The '*survival*' package [23] and *'RColorBrewer'* [24] were used for plotting.

(b) Lab experiment on human detection performance

(i) Stimuli

So that we could assess the effect of target pattern while holding everything else in a given visual scene constant, we used a chroma-key (blue screen) technique. Blue-printed butterfly targets were prepared as per the methods for the first field experiment and photographed *in situ* on bramble plants in the same field site as used for the bird predation experiments. A third of the targets were uniform blue, a third blue with a real hole, and a third blue with a pink patch of the same size and shape as the false holes in the second field experiment, to allow digital replacement with different types of false hole (see below). A total of 150 photographs were taken with a Nikon D3100 digital SLR camera (Nikon Corporation, Tokyo, Japan), including an X-rite ColourChecker

205 Passport (X-Rite, Grand Rapids, MI, USA) for standardising image colours. The
206 lighting conditions were clear skies and bright sunlight.
207
208 A custom MATLAB R2017 script (The Mathworks Inc., Natick, MA, USA) was used
209 to identify the blue butterflies in photographs and replace this hue with 'bramble green',
210 whilst retaining cast shadow, changing gradations of tone, and partial occlusion by
211 vegetation (figure 2). Using the respective photographs, Plain and Real hole treatments
212 were produced. To replicate the Dark False hole and Pale control treatments from the
213 second experiment, shades of grey from that experiment replaced the pink markings. To
214 create an additional false hole treatment (henceforth 'synthetic'), digitally selected
215 patches of adjacent bramble background were pasted into the pink hole marking. If
216 hole-mimicry is the function of dark wing patches, we predicted that a pattern that
217 depicts background vegetation should be even more effective as camouflage. We
218 therefore had five treatments of 25 images each.
219
220 (ii) Participants and Procedures
221 The experiment was performed by 20 male and 20 female participants, and one
222 participant who did not wish to identify as either male or female. The experiment was
223 run after participants had read generic instructions ('find the hidden butterfly') and
224 completed a consent form in accordance with the Declaration of Helsinki. All
225 participants were either postgraduate students or staff from the University of Bristol,
226 and all were naïve to the design of the experiment. The experiment was carried out in a
227 dark room using a laptop computer (MacBook Pro; Apple Inc., Cupertino, CA, USA),
228 running a control program written in MATLAB using the Psychtoolbox library
229 (Psychophysics Toolbox Version 3; [25]; http://psychtoolbox.org). Participants were
230 seated approximately 50 cm from an external display screen, which was a linearized

(gamma-corrected), 22'', 1024 x 768 pixel LaCie Electron 22Blue CRT monitor (LaCie Ltd., London) with a refresh rate of 100 Hz and a mean luminance of 72 cdm^{-2}.

Five practice images were presented to each participant, one randomly selected from each treatment. This practice stage was followed by five experimental blocks of 25 images. A mid-grey screen with a black fixation cross in the centre was displayed before each trial to focus the attention of the participant. Once the target had been selected using the trackpad's cursor, the next fixation cross and image was presented. Each image had a 60 s time-out. The program presented images from the five treatments to participants in an order separately randomised for each participant. Between blocks participants had the option to take a short break, or to continue straight through to the next block. None of the participants took breaks lasting more than 2 min.

(iii) Statistical Analysis

In the third experiment, accuracy was analysed by calculating the centre of a rectangle enclosing the target; a 'hit' was classed as a trackpad click within 5% of the perimeter of this rectangle. The percentage of misses, at just 2.6 % across all trials, was too low to analyse (models did not converge). This indicates that almost all the variation in performance was captured by the response times. Prior to analysing the latter, one 'impossible' value was removed (< 0.1 ms, the 'false start' criterion in an Olympic sprint). Inverse transforming the times normalised residuals from Linear Mixed Models fitted using the R package '*lme4*' [26], with fixed effect treatment and random effect participant. Subsequent pair-wise comparisons used the Tukey method in the '*multcomp*' package [22].

3. Results

257 (a) Field experiment 1

258 The presence of holes in the 'wings' of the targets significantly lowered mortality
259 compared to intact wings, irrespective of the background substrate (figure 3;
260 treatment*substrate interaction: $\chi_2 = 0.52$, d.f. = 1, $p = 0.470$; main effect of holes: odds
261 ratio = 0.65, $\chi_2 = 6.15$, d.f. = 1, $p = 0.013$). There was also an increased chance of
262 predation when attached to twigs versus brambles (odds ratio = 1.46, $\chi_2 = 4.78$, d.f. = 1,
263 $p = 0.029$).

264

265 (b) Field experiment 2

266 Treatments differed significantly (figure 3**;** $\chi_2 = 141.25$, d.f. = 3, $p < 0.001$) with the Real
267 hole treatment having lower mortality than the Intact (odds ratio 0.53, z = 5.45, $p <$
268 0.001) and Pale controls (odds ratio 0.30, z = 10.68, $p < 0.001$), but similar survival to
269 False holes (odds ratio 0.79, z= 1.89, $p = 0.207$). False holes had lower mortality (odds
270 ratio 0.67, z = 3.61, $p = 0.001$) and Pale controls higher (odds ratio 1.77, z = 5.80, $p <$
271 0.001) than Intact wings. Although there is no significant difference between Real and
272 False holes, the 95% confidence intervals for the odds ratio indicates that the survival
273 benefit conferred by False holes is between 62% worse and 1% better than Real holes.

274

275 (c) Lab experiment on human detection performance

276 Response times differed significantly (figure 4; $\chi_2 = 1185.1$, d.f. = 4, $p < 0.001$) with
277 significant differences in the mean response times of all treatments (Tukey tests, all $p <$
278 0.001), apart from synthetic vs real hole (z = 1.35, $p = 0.660$). The Real hole and
279 Synthetic hole treatments were the slowest to be detected, followed by Plain wings and
280 then Dark false holes, with Pale controls the most rapidly detected.

281

282 ## 4. Discussion

283 Over a century after the first speculations about the function of false holes were made
284 by Poulton [6], we present the first empirical evidence that these types of markings
285 provide a significant survival advantage through reduced detectability. Our model
286 'butterflies' were not modelled on a real species but, if they had been, any reduced
287 predation on real and false hole treatments could have been due to dietary conservatism
288 [28]. This is a still a possibility, although rendered less likely by the fact that the Pale
289 control treatment was readily consumed. There are no bramble-green butterflies with
290 light colour patches in the Bristol region [28].
291
292 The first field experiment indicates that real holes in the wings of background matching
293 butterfly-like prey reduce predation by approximately 35% and although,
294 unsurprisingly, an exposed position increased predation risk compared to location
295 among brambles, holes had similar effects on both substrates. Clearly, real holes in a
296 butterfly's wing would negatively affect flight, but the second experiment demonstrates
297 that false holes are almost as effective when it comes to reducing predation. We next
298 discuss possible mechanisms behind this effect, and compare the results from avian and
299 human experiments.
300
301 The second field experiment showed that real holes and dark patches of the same shape
302 and location led to reduced mortality compared to plain intact wings, whereas pale
303 patches led to increased mortality. This suggests that false holes are not effective by
304 virtue of contrast with the green base colour alone, as might be the case if the
305 mechanism was attraction of attention and distraction from the true outline or shape of
306 the target [13,17,29-31]. Instead, a parsimonious explanation is that false, and real,
307 holes act as surface disruptive coloration, disguising the wing surface continuity
308 through creation of false internal edges [13,32]. In principle, contrasting pale holes

could act this way too, through maximum disruptive contrast [13], lateral inhibition or contour capture [30] but, as has been shown for edge-disrupting camouflage [18,33], this would be undermined if the disruptive colour patches themselves attracted attention by virtue of being colours rare in the background.

The term 'false holes' might imply that false depth cues are important. Such cues break up the continuity of the wing surface into multiple depth planes, encouraging incorrect perceptual segregation [13,30,34]. However our result do not allow such an inference. Manipulations such as edge-enhancement around the false hole [13,34,35] would be informative here because, like Cott [13], we consider surface disruption to be the most plausible explanation for the anti-predation benefits of false holes of the type investigated here. Masquerade is another possible function of false holes when combined with leaf mimicry, and the likelihood would increase if damaged leaves were either more common than undamaged or, for other reasons, birds classified damaged leaves as less likely to be leaf-mimicking insects than intact leaf-like objects [4]. However, as there is some evidence that birds use leaf damage as a cue for the presence of insects [10,11], this would be a cost rather than a benefit of hole-mimicry.

When comparing the results of the computer-based search task using human participants and the second avian predation field experiment, we observe some differences in the relative survival of treatments. In both sets of experiments the presence of real holes conferred significant survival benefit relative to targets with intact wings, and pale control markings in the wings led to the highest levels of predation and detection. However, in the computer experiment, while 'false holes' in terms of the 'synthetic' treatment (cutting and pasting of background elements into the 'hole') were as effective as real holes, dark false holes were not (despite being highly

effective in the avian predation experiments). The differences seen in the results most likely reflect the differences in the tasks: whilst the human experiments solely measured detection under focused attention for a narrow range of target types, the avian predators were seeking multiple prey types. Participants in the human experiments, on debriefing, reported that they found themselves "looking for the hole", as 80% of presented images possessed the 'hole' shape (dark, pale, real or synthetic hole treatments) and only in the intact wings treatment was this shape absent. While the background seen through real holes, and the background pasted into synthetic holes, differed for every single replicate, all dark false holes had identical homogeneous coloration, so this pattern was easier to learn in the, highly constrained, human experiment. Birds, seeking multiple prey types (most of which were unlike our targets), and with multiple interruptions to foraging, would not have had the same opportunity to learn such tactics. Conversely, unlike humans in the computer experiment, birds in the field may have additional cues to depth, from parallax and stereopsis, which would limit the effectiveness of false holes at close range.

Empirical research of disruptive theory has previously focused on marginal markings, with much less investigation into the protective benefits that can be provided by internally placed markings [32,36]. Although false holes remain logically distinct from other centrally placed markings, e.g. eye spots and distractive markings [8,17,31], our results add weight to the support of Stevens *et al.* [32] for Cott's [13] proposition that other non-marginal markings can also achieve a significant disruptive effect. This remains true whether 'false holes' are perceived by birds as holes or not, something that awaits further investigation.

Ethics

Experiments approved by the University of Bristol Animal Welfare and Ethical Review Body (birds) and the University of Bristol Faculty of Science Research Ethics Committee (humans).

Data accessibility

Raw data can be accessed from the Dryad data repository at [doi to be added].

Authors' contributions

ICC and LMC conceived the project; ICC, NSS and LMC designed the experiments; ICC and LMC produced the stimuli; NSS and ICC wrote the programs for the blue-screening and human experiment; LMC carried out the experiments, with the help of ICC and KK. LMC wrote the first draft of the ms, with contributions from all authors. All authors gave final approval for publication and agreed to be accountable for all aspects of the content therein.

Competing interests

We have no competing interests.

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References

1. Cuthill IC. 2019. Camouflage. *J. Zool.* **308**, 75-92.

2. Ruxton GD, Allen WL, Sherratt TN, Speed MP. 2018. *Avoiding Attack*. 2nd edition. Oxford: Oxford University Press.

3. Stevens M, Merilaita S. 2008. Animal camouflage: current issues and new perspectives. *Phil. Trans. R. Soc. B* **364**(1516), 423-427.

4. Skelhorn J, Rowland HM, Speed MP, Ruxton GD. 2010. Masquerade: Camouflage without crypsis. *Science* **327**, 51-51

5. Wallace AR. *Proc. Entomol. Soc*. March 4th: IXXX-IXXXi.

6. Poulton EB. 1890. *The colours of animals: their meaning and use, especially considered in the case of insects. The international scientific series, 2nd edn*. London, UK: Kegan Paul, Trench Trübner, & Co. Ltd.

7. Wallace AR. 1967. Mimicry and other protective resemblances among animals. Westminster Review July, 45-129.

8. Stevens M. 2005 The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera. *Biol. Rev*. **80**, 573-588.

9. Stevens M, Ruxton GD. 2014 Do animal eyespots really mimic eyes? *Curr. Zool.* **60**, 26-36.

10. Heinrich B, Collins SL. 1983. Caterpillar leaf damage, and the game of hide-and-seek with birds. *Ecology* **64**(3), 592-602.

410 **11.** Gunnarsson B, Wallin, J, Klingberg J. 2018. Predation by avian insectivores on
411 caterpillars is linked to leaf damage on oak (*Quercus robur*). *Oecologia* **188**(3), 733-
412 741.
413 **12.** Thayer GH. 1909. *Concealing-coloration in the animal kingdom: an exposition of the*
414 *laws of disguise through color and pattern: being a summary of Abbott H. Thayer's*
415 *discoveries*. New York, NY: Macmillan.
416 **13.** Cott HB. 1940. *Adaptive coloration in animals*. London: Methuen & Co. Ltd.
417 **14.** Merilaita S, Scott-Samuel NE, Cuthill IC. 2017. How camouflage works. *Phil. Trans.*
418 *R. Soc. B* **372**, 20160341. (doi:10.1098/rstb.2016.0341).
419 **15.** Stevens M, Párraga CA, Cuthill IC, Partridge JC, Troscianko TS. 2007. Using digital
420 photography to study animal coloration. *Biol. J. Linn. Soc*. **90**(2), 211-237.
421 **16.** Stevens M, Cuthill IC. 2006. Disruptive coloration, crypsis and edge detection in
422 early visual processing. *Proc. R. Soc. B* **273**(1598), 2141-2147.
423 **17.** Stevens M, Graham J, Winney IS, Cantor A. 2008. Testing Thayer's hypothesis: can
424 camouflage work by distraction? *Biol. Lett*. **4**(6), 648-650.
425 **18.** Stevens M, Cuthill IC, Windsor AMM, Walker HJ. 2006. Disruptive contrast in animal
426 camouflage. *Proc. R. Soc. B* **273**, 2433-2438
427 **19.** Hart NS, Partridge JC, Cuthill IC, Bennett ATD. 2000. Visual pigments, oil droplets,
428 ocular media and cone photoreceptor distribution in two species of passerine bird: the
429 blue tit (*Parus caeruleus* L.) and the blackbird (*Turdus merula* L.). *J. Comp. Physiol.*
430 *A* **186**(4), 375-387.
431 **20.** Therneau TA. 2018. coxme: Mixed Effects Cox Models. R package version 2.2-10.
432 <URL: https://CRAN.R-project.org/package=coxme>
433 **21.** Ruxton GD, Beauchamp G. 2008. Time for some a priori thinking about post hoc
434 testing. *Behav. Ecol*. **19**(3), 690-693.

435 **22.** Hothorn T, Bretz F, Westfall P. 2008. multcomp: Simultaneous inference in general
436 parametric models. R package version. *Biom. J.* **50**, 346-363.
437 **23.** Therneau TM. 2015. A Package for Survival Analysis in S. version 2.38, <URL:
438 https://CRAN.R-project.org/package=survival>
439 **24.** Neuwirth E. 2014. RColorBrewer: ColorBrewer palettes. R package version 1.1-2.
440 <URL: https://cran. r-project. org/package= RColorBrewer>
441 **25.** Brainard DH, Vision S. 1997. The psychophysics toolbox. *Spatial Vision* **10**, 433-
442 436.
443 **26.** Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects
444 Models using lme4. *J. Stat. Softw.* **67**(1), 1-48.
445 **27.** Marples NM, Roper TJ, Harper DGC. 1998. Responses of wild birds to novel prey:
446 evidence of dietary conservatism. *Oikos* **83**, 161-165.
447 **28.** Barnett R, Higgins R, Moulin T, Wiltshire C. 2003. *Butterflies of the Bristol Region:*
448 *The Wildlife of the Bristol Region: 2*. Bristol: BRERC Publications.
449 **29.** Dimitrova M, Stobbe N, Schaefer HM, Merilaita S. 2009. Concealed by conspicuousness:
450 distractive prey markings and backgrounds. *Proc. R. Soc.. B* **276**, 1905-1910.
451 **30.** Troscianko T, Benton CP, Lovell PG, Tolhurst DJ, Pizlo Z. 2009. Camouflage and visual
452 perception. *Phil. Trans. R. Soc. B* **364**, 449-461.
453 **31.** Olofsson M, Dimitrova M, Wiklund C. 2013. The white 'comma' as a distractive mark on the
454 wings of comma butterflies. *Anim. Behav.* **86**, 1325-1331.
455 **32.** Stevens M, Winney IS, Cantor A, Graham J. 2008. Outline and surface disruption in animal
456 camouflage. *Proc. R. Soc. B* **276**(1657), 781-786.
457 **33.** Fraser S, Callahan A, Klassen D, Sherratt TN. 2007. Empirical tests of the role of disruptive
458 coloration in reducing detectability. *Proc. R. Soc. B* **274**, 1325-1331.

34. Egan J, Sharman RJ, Scott-Brown KC, Lovell PG. 2016. Edge enhancement improves disruptive camouflage by emphasising false edges and creating pictorial relief. *Sci. Rep.* **6**, 38274.

35. Koenderink JJ. 1998. Pictorial relief. *Phil. Trans. R. Soc.* A **356**(1740), 1071-1086.

36. Stevens M, Merilaita S. 2009. Defining disruptive coloration and distinguishing its functions. *Phil. Trans. R. Soc. B* **364**(1516), 481-488.

Figures

Figure 1 Examples of false holes found in Lepidoptera and Anura respectively. Top Left: *Siculodes aurorula* (Thyrididae) © Photo courtesy of Marcos Cesar Campis, Morro Agudo, Brazil. Bottom Left: *Siculodes aurorula* (Thyrididae) © Photo courtesy of Pavel Kirillov, Comadre, Limon, Costa Rica; Top and Bottom Right: *Rhinella margaritifera*, Crested Forest Toad, © Photo courtesy of John Sullivan/Ribbit Photography, Madre Selva Biological Station, Loreto, Peru.

476

477

478 **Figure 2** Left: target dimensions, illustrated with a Pale control treatment; the holes were
479 absent for the intact wings treatment. The approximate point of pin insertion is indicated
480 (•) on the midline. Distances A (between centre points of each hole) and B (between the
481 centre point of each hole to the midline) were always consistent. Right: (a) Blue target in
482 situ; (b) blue replaced with 'bramble green' by means of chroma-key to form an Intact
483 treatment; (c) Real hole; (d) Pale control; (e) dark false hole; (f) Synthetic false hole.
484 Panels (c) to (f) are close-ups; the image size in the human experiment was as in (b).

485

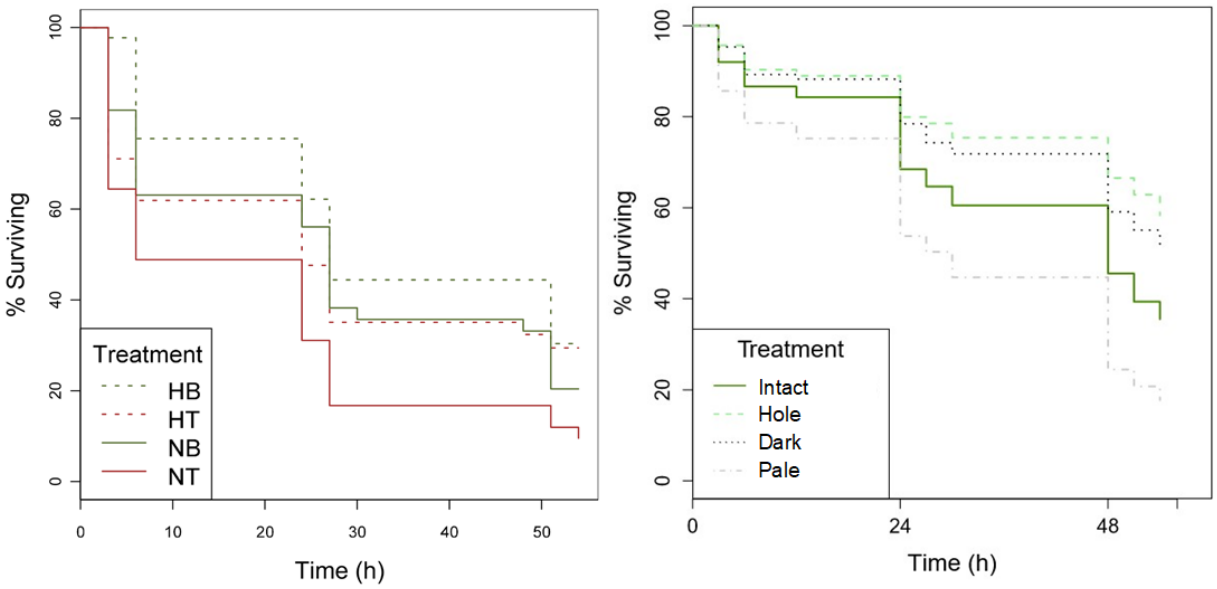

Figure 3 The left-hand plot shows, for the first field experiment, survival on each substrate (top to bottom: wings with holes on bramble (HB), wings with holes on twigs (HT), intact wings on bramble (NB), and intact wings on twigs (NT)). The right-hand plot shows survival in the second field experiment, for the four treatments (Intact wings, Real holes, Dark false hole, and Pale false holes) on a bramble substrate. The curves indicate the probability of avoiding bird predation as a function of time over a three-day period (54 h), based on Kaplan–Meier estimates to account for incomplete data due to censoring. Long periods of stasis (8+ h) with no changes in survival probability corresponds to hours of darkness when targets were not checked.

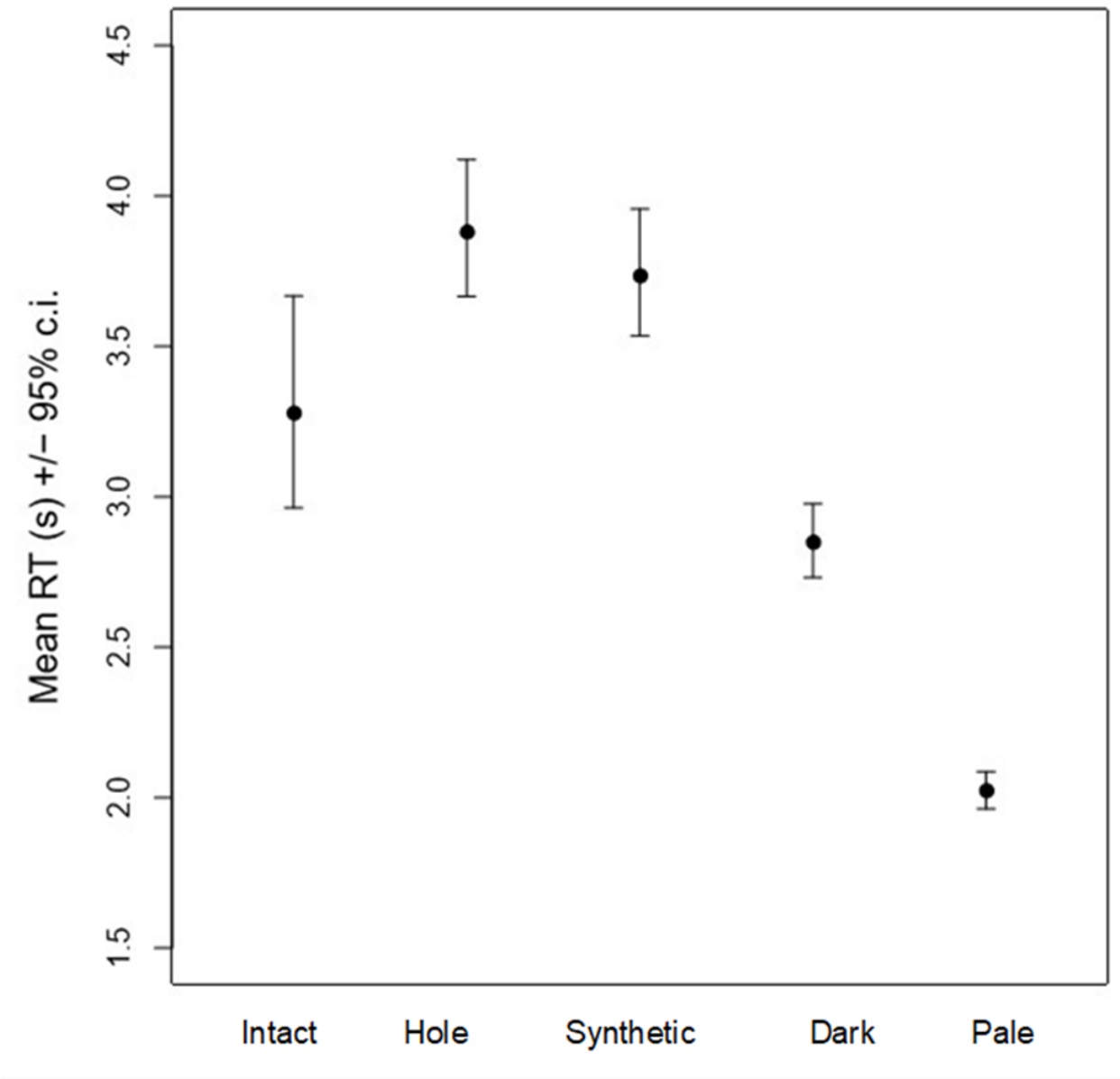

Figure 4 Mean (± 95% c.i., based on fitted GLMMs) reaction times (in seconds) by human participants in the lab experiment. Greater reaction times indicate increased difficulty of detection and hence more effective target camouflage.